Technical Report No. 64

SEASONAL ABUNDANCES OF THE MAMANE MOTH, ITS NUCLEAR POLYHEDROSIS VIRUS, AND ITS PARASITES

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U. S. International Biological Program

May 1975

ABSTRACT

The mamane moth (Uresephita polygonalis, Denis and Schiff.) is a serious pest of the mamane tree (Sophora chrysophylla, Salisb.) on the island of Hawaii. The larvae of this moth feed on mamane leaflets sometimes causing serious defoliation.

The life cycle and development of U. polygonalis were determined by observation of laboratory reared animals. Results of laboratory tests indicated that Acacia koa was not a host of the larvae.

Seasonal abundance of the moth was estimated from monthly counts of eggs and larvae collected from four sampling sites. Apparently there are no positive correlations of population dynamics with rainfall, humidity, temperature and vegetative flushing of mamane.

Four parasites were reared from U. polygonalis collected at the sampling site. Only one of these, an ichneumonid (Horogenes blackburni, Cameron) appeared to be an important parasite, although it did not occur in high enough numbers to seriously affect mamane moth populations.

The nuclear polyhedrosis virus, present only at sampling site 4, was a major factor in the regulation of the U. polygonalis population at that site. Laboratory tests indicated that larvae from all sites were highly susceptible to the virus. However, why the virus did not occur at all sites remains to be determined. Possibly the amount of sunlight and ultraviolet radiation reaching the trees and ground beneath them affects the virus which is inactivated by light. Thus, in years when U. polygonalis populations do not reach high levels, the virus is confined to cloud covered areas such as site 4. The virus disease plays a major role in population regulation when it reaches epizootic levels.

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INTRODUCTION

The mamane moth, Uresiphita polygonalis (Denis and Schiffermueller) Zimmerman[1], is a serious pest of the mamane tree, Sophora chrysophylla (Salisb.), on the island of Hawaii. It was first collected in the islands by Blackburn before 1881 at Haleakala, Maui, at an elevation between 1220 and 1520 meters (4000-5000 ft). It was originally described as an endemic species, Mecyna virescens, by Butler in 1881. Zimmerman (1958) discovered that it was an European species, for which the correct name was Uresiphita polygonalis.

Uresiphita polygonalis is the combination currently used for this species. However, Hannemann (1964) uses the name U. limbalis (Denis and Schiff.) with polygonalis as a form.

There are many synonyms, the most important of which are cited by Zimmerman (1958) as follows:

Pyralis polygonalis (Denis and Schiffermueller (1775)).

Mecyna polygonalis (Huebner) Meyrick (1890).

Pyralis limbalis (Denis and Schiffermueller (1775)).

Uresiphita limbalis (Denis and Schiffermueller) Huebner (1825).

Mecyna virescens Butler (1881). Meyrick (1888); (1889). Hampson (1899).

Other synonyms were provided by Dr. J. D. Bradley, Lepidopterist, Commonwealth Institute of Entomology, London, that are not included in Zimmerman"s (1958) work. These synonyms were enclosed in a personal communication from A. H. Parker, Assistant Director, Commonwealth Institute of Entomology, London:

U. aversalis Guenee (1854).

U. carbonalis Caradja (1939).

U. deprivalis Walker (1859).

U. diversalis Huebner (1796).

U. gilvata F. (1794).

U. gracilis Caradja (1916).

U. rusticalis Huebner (1796).

U. teriadalis Guenee (1854).

U. villicalis Huebner (1825).

Both Zimmerman (1958) and Hannemann (1964) mentioned host plants and presented figures of genitalia. In England, Zimmerman (1958) said that this pyralid fed on

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[1] Lepidoptera: Pyraloidea: Pyralidae: Pyraustinae.

Genista, Cystisus and also on legumes. In Hawaii, Perkins (1913) cited mamane as its favorite food plant, but also mentioned that the larvae fed on Acacia koa Gray and that the moth sometimes occurred at low elevations in places where no mamane grew. During the course of this investigation a host range test was performed using A. koa phyllodes and juvenile leaves. Results indicated Acacia koa is not a host plant. In Hawaii, mamane seems to be its only host.

Mamane is an attractive forest tree which supports several species of native animals. Oechalia bryani Usinger, an endemic predacious pentatomid (Zimmerman, 1948) and large endemic colorful cerambycids (Gressitt and Davis, 1972) are among the unique insects closely associated with the tree.

The mamane is by far the most important plant to the Palila, Psittirostra bailleui, an endangered endemic bird that feeds on the green seed pods. The 'Elepaio, Chasiempis sandwichensis, another endemic bird, flies and hops from branch to branch of the mamane gleaning insects from leaves and stems. Other endemic birds (the 'I'iwi, Vestiaria coccinea, the 'Apapane, Himatione sanguinea, and the 'Amakihi, Loxops virens) are honeycreepers that feed on the nectar of the mamane's yellow flower clusters. The endemic 'Akiapola'au, Hemignathus wilsoni, feeds on woodboring insects it finds on or in the trunks and larger branches. The Japanes White-eye, Zosterops japonica, is an exotic bird that flits among the branches of mamane feeding primarily on insects and taking a little nectar. Another exotic bird thought to be associated with mamane is the House Finch, Carpodacus mexicanus, which is abundant in mamane forests. It is primarily a seed eater although it has been reported to also feed on buds.

Mamane has been found on all the major islands (Neal 1965): Kauai, Oahu, Molokai, Lanai, Maui and Hawaii. Neal (1965) and Degener (1945) stated that it is not found on Molokai, but J. W. Beardsley has reported it growing on that island (pers. comm.). Mamane grows at altitudes between 300 and 2900 m (1000 and 9500 ft). It occurs as a shrub, a sprawling tree, or as an erect tree up to 12 m (40 ft) high. The leaves are 12.7 to 15.2 cm (5-6 in) long; each usually having from 13 to 21 oblong leaflets that generally measure about 2.5 cm (1 in) long and about 1.3 cm (0.5 in) wide. The leaflets can be directly opposite or alternate with each other. Older leaflets are smooth but the new leaves have a dense covering of yellow or whitish hairs especially on the lower surface. The yellow flowers are about 2.5 cm (1 in) long and bloom in small groups on the tips of branches or in leaf axils. The mature seed pods are usually about 12.7 cm (5 in) long and 1.3 cm (0.5 in) wide and carry about 7 seeds that are orange or a darker yellow than

the flowers when mature (Neal, 1965).

U. polygonalis is a major pest of mamane. The larvae feed on the leaves and at times can completely defoliate a tree. Trees that are heavily infested show a considerable amount of webbing. The leaves inside larval tunnels and those connected to these webs are nearly all eaten off. Continued defoliation can result in the tree dying or becoming seriously weakened so that it may succumb to disease.

Very little is known about the seasonal abundance or the factors that affect the abundance of this important insect on mamane. This study was undertaken to attempt to identify some of the factors regulating populations of Uresiphita polygonalis.

MATERIALS AND METHODS

Study Sites

This study was carried out using mamane trees on the island of Hawaii. Four sampling sites were chosen and trees used were randomly selected each time at each site. Three of the four sites were located off the Mauna Loa Strip Road. Site 1 was beyond the end of the road at 2210 m (6600 ft). Site 2 was at 1650 m (5400 ft) and Site 3 was off the lower portion of the road at an elevation of 1280 m (4200 ft). Site 4 was at 1680 m (5500 ft) on Mauna Kea off the Saddle Road, 13.7 km (8.5 mi) from the junction of Saddle Road and the highway going into Kamuela from Kona.

Sampling Methods

Sampling by vacuuming foliage with a D-VAC collecting apparatus, beating off with a net or shaking foliage over a sheet did not present an adequate picture of the population. These methods left eggs on the leaves or early-instar larvae in the webbing or missed the older larvae that dropped to the ground as soon as any part of the tree near them was disturbed.

The technique utilized involved quickly covering the selected foliage with a plastic bag 71 cm long and 56 cm wide and then cutting the sample from the tree. The bag was then tied and brought back to the laboratory for investigation.

A preliminary study was undertaken April 29, 1971, at a location that showed a large population of U. polygonalis, to determine the best sampling height levels

on a tree. At this time the population had either just reached peak numbers for that season or was already declining. Ten trees, each approximately 9 m (30 ft) tall, were selected. Each tree was divided into 3 levels, each level measuring 3 m (10 ft) in height. Several twigs were bagged from each of the 3 levels on each of the 10 trees. Egg and larval counts were made and comparisons per unit area of leaf surface were made.

Observations showed that the adult female preferred to oviposit on new growth at the tips of terminal branches. Larvae preferred feeding on the young tender foliage, but when the population was high the larvae could be found feeding on old as well as new foliage on all parts of the tree and female moths oviposited on older leaflets. The level nearest the ground contained the highest number of eggs and larvae.

The seasonal abundance of U. polygonalis was estimated by making monthly counts of eggs and larvae on samples of new growth at the tips of several terminal branches 0.6 to 2.4 m (2-8 ft) off the ground. Ten trees were sampled at each of the study sites.

After the counts were made, the eggs and larvae were separated from the foliage and the immatures were reared at 21°C (70°F) and 50% relative humidity in 14 gm (8 oz) cardboard cups containing fresh mamane foliage. These containers were covered with a petri dish to permit easy observation. These observations yielded data on the parasitization and disease incidence in the population. Fresh mamane leaves were used as larval food and introduced every other day. Adults were fed a solution of one part honey to four parts water.

Mamane was not always easily available, therefore two artificial diets were tried--a modification of Harley's formulation (Wesson, 1932) and a pinto bean diet formulation (Bill Rose pers. comm.). Both were obtained from the State of Hawaii Exploratory Entomologist Bill Rose. Three hundred 1st-instar larvae were divided into groups of one hundred. These three groups were in turn divided into groups of ten in separate 14 gm (8 oz) containers with petri dish lids and supplied with the following foods: a 2 gram portion of the modified Harley's diet, a 2 gram portion of the pinto bean diet, and 2 grams of mamane leaves. All of the larvae on both artificial diets died within six days; only a few reached the second instar. Only 14 of the larvae raised on mamane leaves died.

Acacia koa was also tested as a possible host for the larvae. Three hundred 1st-instar larvae were used and were placed 10 to a container in a manner similar to the test of the artificial diet. One hundred were put on mamane; another

hundred were placed on the juvenile leaves of Acacia koa and another hundred were put on A. koa phyllodes.

Most larvae on A. koa died the second day of the test. The last of these died the 6th day. Two containers of juvenile leaves showed signs of slight feeding. Nineteen of the larvae raised on mamane died of unknown causes, the rest were reared out to adults. The results indicated that the larvae could not be reared on the artificial diets and A. koa, so mamane was used for all rearing.

Since all population data were based on numbers per given surface area of leaf, the surface area of the leaves had to be determined. However, it was impractical to determine the leaf surface area in each sample by measuring the leaves. Calculating the surface area using a ratio of fresh weight to surface area was impractical because the fresh leaves lost water so fast a constant weight could not be derived.

To obtain a constant weight, a Precision Scientific Freas Model 845 drier was used to eliminate the water. The relationship between dry weight and the leaf surface area was derived by placing fresh leaves on light sensitive Kodak Processing Paper and placing a heavy glass plate over the leaves to prevent their movement. The paper was then exposed to the light and developed. The area on the paper not covered by the leaves darkened and the areas under the leaves remained white, tracing a perfect outline for the leaf. These leaf images were cut out and weighed. This weight when correlated with the weight of a similar piece of paper with a known surface area gave the surface area of the fresh leaves. This figure was doubled to account for the top and bottom surface areas of a leaf. The calculated surface area of the fresh leaves was then correlated to their dry weight so that the surface area of the fresh leaves could be calculated from their dry weights.

In practice, leaves in a sample were stripped from their branches, placed in the drier at 150°C for two days, taken out and weighed. This dry weight was converted to leaf surface area. The numbers of eggs and larvae were recorded with the leaf surface area for every sample.

To determine relationships of the abundance of U. polygonalis to monthly precipitation, monthly humidity and mean monthly temperatures, abundance was plotted against monthly values for rainfall, humidity, and temperature. Abundance was also plotted against index values for vegetative flushing of mamane which were obtained from Lamoureux (1973).

A nuclear polyhedrosis virus (NPV) and several parasites were found to attack

U. polygonalis. To evaluate the effectiveness of these organisms as biological control agents, eggs and larvae collected each month were reared in the laboratory. In late summer, fall, and winter months the numbers of U. polygonalis collected were so few that additional larvae were collected to supplement those taken in samples. However, even supplemental collecting became difficult as larvae grew increasingly hard to find during the fall and winter. The number of larvae parasitized or diseased in the samples as determined by laboratory rearings was recorded.

Since the NPV was found only in the larvae collected off the Saddle Road (Site 4) and not in the Mauna Loa population, several tests were conducted to determine whether the Mauna Loa population was susceptible to the virus.

Bodies of five hundred late-instar larvae that had died of the disease were pulverized and diluted with distilled water. A solution of polyhedra was isolated, clarified, and purified by filtration through cheese cloth, and then centrifuged to obtain a white precipitate of polyhedra. The supernatant was drawn off. The precipitate was diluted with three milliliters of distilled water and shaken to obtain a uniform polyhedral suspension. Forty 3rd-instar larvae from the same egg mass were divided into two groups of twenty. Third-instar larvae were used for ease of autopsy.

Two drops of the polyhedral suspension were placed on each of twenty leaf halves. The suspension was allowed to dry on the leaf halves. The contaminated leaf sections were placed, one per container, in the twenty 14 gm (8 oz) cardboard containers. One larva was placed in each container. In every case, the larva completely ate the contaminated leaf. Thereafter the larvae were raised on virus free mamane leaves.

As a control twenty larvae of the second group were placed individually in twenty 14 gm (8 oz) cardboard containers. Two drops of distilled water were put on each of the halves of ten mamane leaves. The distilled water was allowed to dry. Each half leaf was fed to a caterpillar in the second group. None of the control larvae became infected while all of the treated larvae died from an NPV infection.

The first expression of symptoms in treated larvae was delayed development; the length of larval stadia was increased. The diseased larvae were smaller than healthy larvae of the same age. They became white beneath the integument, due to the masses of polyhedra present. Many larvae climbed to the top of their container and died hanging by their prolegs. Finally the larval skins became

fragile sacks, broke open and their contents flowed out. All the larvae of the first group died within eleven days after showing the first symptoms. Autopsy revealed the bodies of these larvae were loaded with polyhedra.

RESULTS

Life Cycle and Description of Stages

Continuous generations of U. polygonalis were raised in the laboratory from April, 1971 until August, 1975 at 21°C (70°F) and about 50% relative humidity.

Adults were small, about 16 millimeters long, gray-black or brown-black moths. The sex-ratio of the moths raised from 344 eggs very closely approximated 1:1 with 174 (50.6%) females and 170 (49.4%) males. The chi-square test was consistent with the hypothesis of a 1 to 1 ratio of male to female moths ($P < 0.995$). At the above temperature the female has a preoviposition period of about three to five days. Eggs were about one millimeter in diameter and were laid in masses up to 73 eggs with an average of 24 eggs. The female initially laid eggs in a small mass from one to five eggs. Later they laid in larger masses usually numbering from 20 to 30 eggs. The flat, oval, white egg mass was formed by the overlapping of rows of flat scale-like eggs. The female may deposit an average of 200-300 eggs over a 4- to 10-day period.

On the 3rd day after oviposition black head capsules of the 1st-instar larvae appeared; and movement could be seen through the egg chorion. Eggs hatched on the 4th day after oviposition . The newly emerged white larvae had 3 pairs of thoracic legs, 4 pairs of ventral prolegs and 1 pair of anal prolegs. The most noticeable markings were the black cervical shield behind the black head capsule and the black spots associated with the long setae. On each side of the larva there were two longitudinal rows of black chalazae, one in the subdorsal area and one row in the supraspiracular area. On the mesothorax and metathorax there was one chalaza per row, each with two simple setae. On the abdominal segments the subdorsal row had two chalazae per segment, each with one simple seta. The supraspiracular row had one chalaza per segment, each with one simple seta. Setation on the body as a whole was sparse, the most noticeable being long white simple hairs. Crochets on ventral prolegs were arranged in a triordinal, uniserial, mesal penellipse. The larvae were 2 millimeters long. The larvae fed gregariously: they usually bound adjacent leaves together and fed protected between them, skeletonizing the leaf

surface but not eating entirely through the leaf.

On the 4th or 5th day after hatch the larvae molted into green caterpillars 4 millimeters long with light brown head capsules. The cervical shield then had a mid-dorsal white stripe running from its anterior edge to its posterior edge with a white spot on each side of the stripe. Chalazae were darker than those on the 1st instar. By this time the larvae had usually eaten the leaves first fed upon and either migrated to adjacent leaves or dropped to other branches on silk threads. The 2nd larval stage lasted 4 or 5 days.

The 3rd instar is 7 millimeters long. The 3rd-instar larva as well as later instars no longer fed gregariously, but fed in silk-lined tunnels which they formed by drawing the leaves inward with webbing. The larvae no longer skeletonized the leaves and ate from the leaf margin inward. When slightly disturbed these and older larvae crawled into their tube webs, and if the disturbance was severe enough they dropped to the ground. Younger larvae also retreated into their web when disturbed slightly but dropped to safety if further prodded.

After another 3 to 4 days the larva molted into the 4th instar which was 11 millimeters long. The two white spots on each chalaza of the dorsal row, one on the dorsal side and one on the ventral, became more evident than they were in the third instar. On the whole, markings of the 4th instar were more striking; the black and green darkened and the black increased between chalazae of the two rows. The 4th larval stage lasted for 4, 5, or 6 days. The 5th-instar larva was about 13 millimeters long.

The 5th instar lasted 5 to 6 days. The 6th instar was 21 millimeters long. Coloration continued to darken and the markings stood out more, especially the black and the subspiracular longitudinal yellow-white which reaches from the head until almost the tip of the abdomen. The space between the rows of chalazae turned brownish on each side. The 6th-instar larva actively fed for 5 or 6 days. When ready to pupate it crawled down or dropped off the tree and found a suitable pupation site beneath leaf litter or debris or under rocks on the ground beneath the tree. The larva's body browned, and it showed sluggish prepupal behavior for 1 to 3 days. Its body shortened and it pupated.

The pupa was dark brown, 13 millimeters long and rapidly moved its abdomen if disturbed.

After a 14 to 16 day pupal period the adult emerged. The wing expanse was

about 32 millimeters. Adult coloration varied widely in the field at all locations. Adults were dark brown, or grey and black spotted or mottled. Grey, brown, and black were combined in many different mottled patterns and irregular bands on the front wings. At rest the wings were held out flat over the abdomen with the anal margins of the front wings touching and running the length of the abdomen. The pale brown hind wings had a wide fringe on their apical and anal margins.

The labial palps were very prominent and pointed, so when viewed from above the moth had the shape of an arrowhead. They moved in a quick, jerky, zigzag flight, usually for short distances and were frequently active during the day.

Seasonal Abundance

Figure 1 presents the total number of larvae taken in samples from each of the four sites. Table 1 shows data according to the various developmental stages collected in the samples. Figure 1 shows that at the end of April in 1971, when sampling was started, the pest population was scarcely discernible at site 1, not evident in May, but definitely established in June, increasing until it reached a peak in the beginning of July. The site 1 population dropped off to zero in mid-July when no larvae were recovered.

At the end of April, 1971 the site 2 population was either at a peak or already declining, and the decline continued until mid-August when no larva was taken in the samples. Numbers of larvae in samples from site 3 indicate that this population was at its highest point or declining at the end of April, 1971. Larval counts continued to decline until the beginning of August when no larva was collected in samples. At site 4, larvae were present in considerable numbers in April and May, and were most abundant in mid-June. The population dropped slowly throughout July and larvae disappeared from the samples in early August.

The peaks in the populations in sites 1 and 4 seemed to coincide (June-July), although the site 4 population started increasing before that of site 1. In both years sampled, site 1 had a higher population than site 4. The peaks in the populations at sites 2 and 3 also coincided with each other but occurred in April and May, a couple of months before those of sites 1 and 4.

Significantly, however, although the populations peaked at different times, they all declined sharply at about the same time in August. This occurred in both years sampled. Only two larvae were picked up in samples during August,

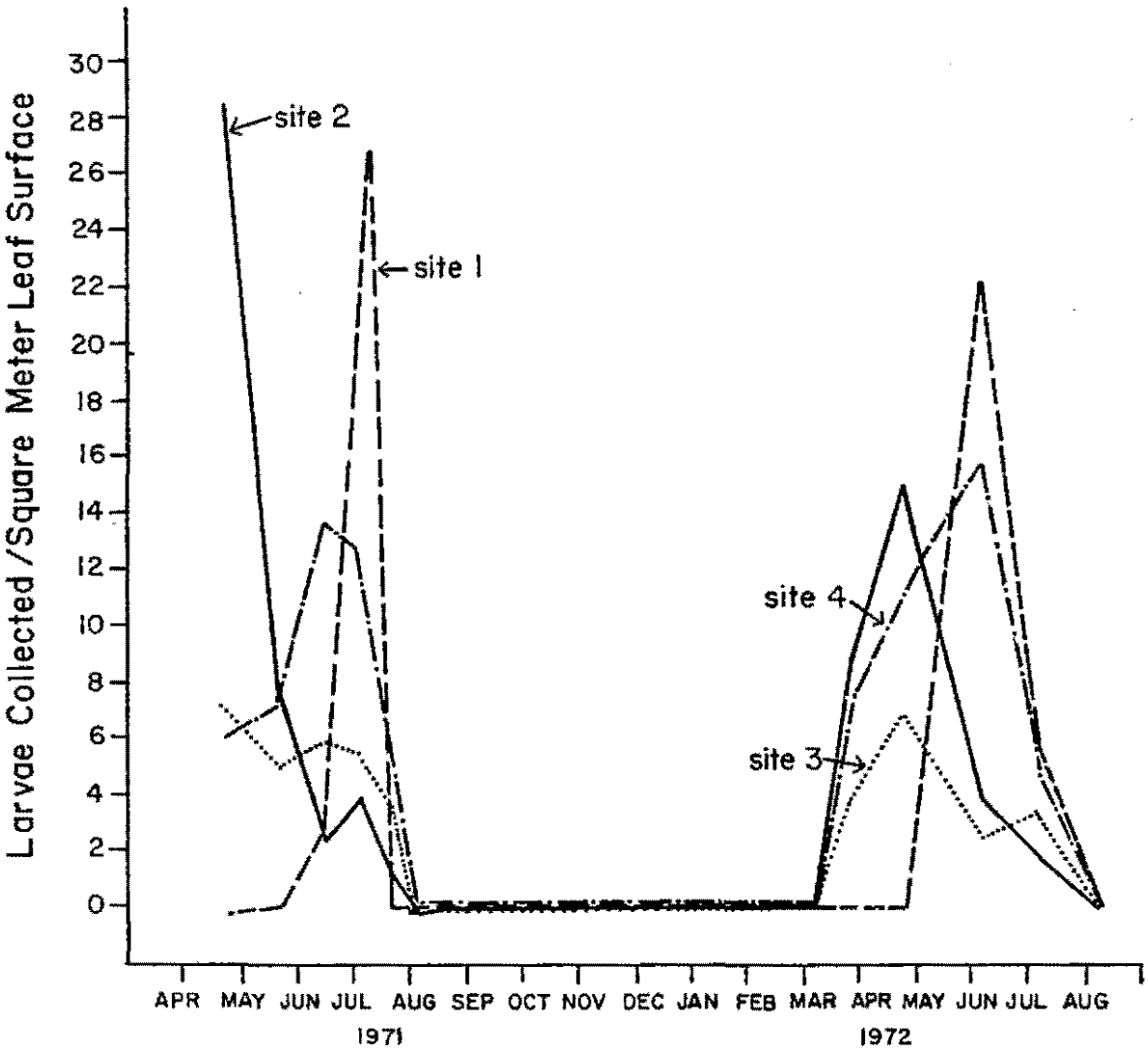

FIG. 1. Seasonal abundance of U. polygonalis larvae on mamane, 1971-72.

TABLE 1. Sampling data of U. polygonalis immature stages for each site.

Site No. 1 2210 m (6600 ft) Mauna Loa									Site No. 2 1650 m (5400 ft) Mauna Loa							
Date	Total Larvae	6th Instar	5th Instar	4th Instar	3rd Instar	2nd Instar	1st Instar	Eggs	Total Larvae	6th Instar	5th Instar	4th Instar	3rd Instar	2nd Instar	1st Instar	Eggs
4/29/71	1	-	-	-	-	-	1	-	59	2	13	16	21	7	-	-
5/21/71	-	-	-	-	-	-	-	-	18	2	3	2	5	2	4	-
6/15/71	8	-	-	1	-	5	2	-	5	3	1	1	-	-	-	35
7/3/71	63	-	1	-	3	19	40	-	9	1	-	1	3	4	-	-
7/17/71	-	-	-	-	-	-	-	-	3	-	1	-	2	-	-	19
8/3/71	-	-	-	-	-	-	-	-	2	-	-	-	-	2	-	-
8/18/71	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8/31/71	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
10/3/71	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
10/30/71	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12/5/71	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1/29/72	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3/5/72	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3/20/72	-	-	-	-	-	-	-	-	22	-	-	-	3	11	8	-
4/29/72	-	-	-	-	-	-	-	-	34	2	1	4	8	13	6	8
6/3/72	49	-	-	5	15	3	26	-	8	1	2	4	1	-	-	16
7/5/72	14	-	-	-	1	4	9	23	4	2	2	-	-	-	-	-
8/4/72	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

TABLE 1 Continued.

Site No. 3 1280 m (4200 ft) Mauna Loa									Site No. 4 1680 m (5500 ft) Mauna Kea								
Date	Total Larvae	6th Instar	5th Instar	4th Instar	3rd Instar	2nd Instar	1st Instar	Eggs	Date	Total Larvae	6th Instar	5th Instar	4th Instar	3rd Instar	2nd Instar	1st Instar	Eggs
4/29/71	17	-	-	-	4	13	-	-	4/28/71	14	-	3	1	2	8	-	-
5/21/71	12	2	-	1	6	3	-	-	5/20/71	13	-	-	-	5	6	2	-
6/15/71	15	3	1	-	1	3	7	-	6/13/71	38	8	2	2	10	13	3	-
7/3/71	13	-	-	2	-	4	7	-	7/5/71	29	3	7	2	5	8	4	-
7/17/71	9	-	-	1	-	-	8	17	7/19/71	16	-	3	2	2	7	2	-
8/3/71	-	-	-	-	-	-	-	-	8/4/71	-	-	-	-	-	-	-	-
8/18/71	-	-	-	-	-	-	-	-	8/19/71	-	-	-	-	-	-	-	-
8/31/71	-	-	-	-	-	-	-	-	9/1/71	-	-	-	-	-	-	-	-
10/3/71	-	-	-	-	-	-	-	-	10/2/71	-	-	-	-	-	-	-	-
10/30/71	-	-	-	-	-	-	-	-	10/31/71	-	-	-	-	-	-	-	-
12/5/71	-	-	-	-	-	-	-	-	12/4/71	-	-	-	-	-	-	-	-
1/29/72	-	-	-	-	-	-	-	-	1/30/72	-	-	-	-	-	-	-	-
3/5/72	-	-	-	-	-	-	-	-	3/4/72	-	-	-	-	-	-	-	-
3/30/72	8	-	-	1	4	1	1	31	3/31/72	16	-	-	-	-	-	16	-
4/29/72	15	4	-	1	8	-	2	-	4/30/72	24	-	2	9	7	4	2	-
6/3/72	5	1	1	-	3	-	-	53	6/4/72	35	11	5	9	2	1	7	-
7/5/72	7	1	3	3	-	-	-	-	7/6/72	11	3	4	4	-	-	-	-
8/4/72	-	-	-	-	-	-	-	-	8/5/72	-	-	-	-	-	-	-	-

both at site 2 at the beginning of that month. No larvae were collected in the samples after the middle of August. In the following year, no larvae were found in samples until the end of March, although five adults were seen at site 2 early in the month. Larval counts again started to increase at sites 2, 3, and 4 at the end of March reaching peaks at sites 2 and 3 at the end of April. The population at site 4 reached its highest level at the start of June, 1972.

In early June, 1972, larval numbers were declining at sites 2 and 3, and by the beginning of July, 1972, the populations at all sample sites showed a decline. This situation may be compared to the similar decline which occurred the previous year around the middle of July, 1971.

It is apparent that at high elevations, populations of U. polygonalis appear and explode over a short period of time. The numbers collected per sample, therefore, in those samples that contain larvae are higher than those from the lower elevations. The appearance of U. polygonalis at the lower elevations was spread over a longer period of time and the population during the peak period was not as high as at the higher elevations. The largest numbers of larvae were collected at 1680 and 1650 m (5500 and 5400 ft).

In the fall and winter months adults, eggs, and larvae of different stages were observed and collected in small numbers by carefully searching the trees at all sites as well as other localities around the island. In early October, one egg mass, three adults, and ten 2nd-instar larvae were picked up at site 4; two egg masses were collected at site 1; and four 2nd-instar larvae were collected at site 3. In late October, two 4th-instar and one 6th instar larvae were collected at Kilohana near site 4. In December, forty-six 1st-instar larvae were found between two leaves webbed together at site 2. In January at Kilohana, one 4th, two 5th, and one 6th instar were collected. These larvae collected during fall and winter indicate a stationary multivoltine population below 1830 m (6000 ft) with considerable overlapping of generations. The population does not hibernate but rather maintains itself at very low numbers at elevations lower than 1830 m (6000 ft) until conditions in spring are right for another population increase.

Figures 2, 3, and 4 present National Park Service and International Biological Program records for the total monthly precipitation, mean monthly temperatures, and monthly humidity means, with the seasonal abundance of larvae from sampling sites 1, 2, and 3 respectively. Monthly rainfall records for the Mauna Loa sites were derived from rainfall records obtained weekly at stations on the Mauna Loa Strip Road. Mean monthly temperatures and monthly percent

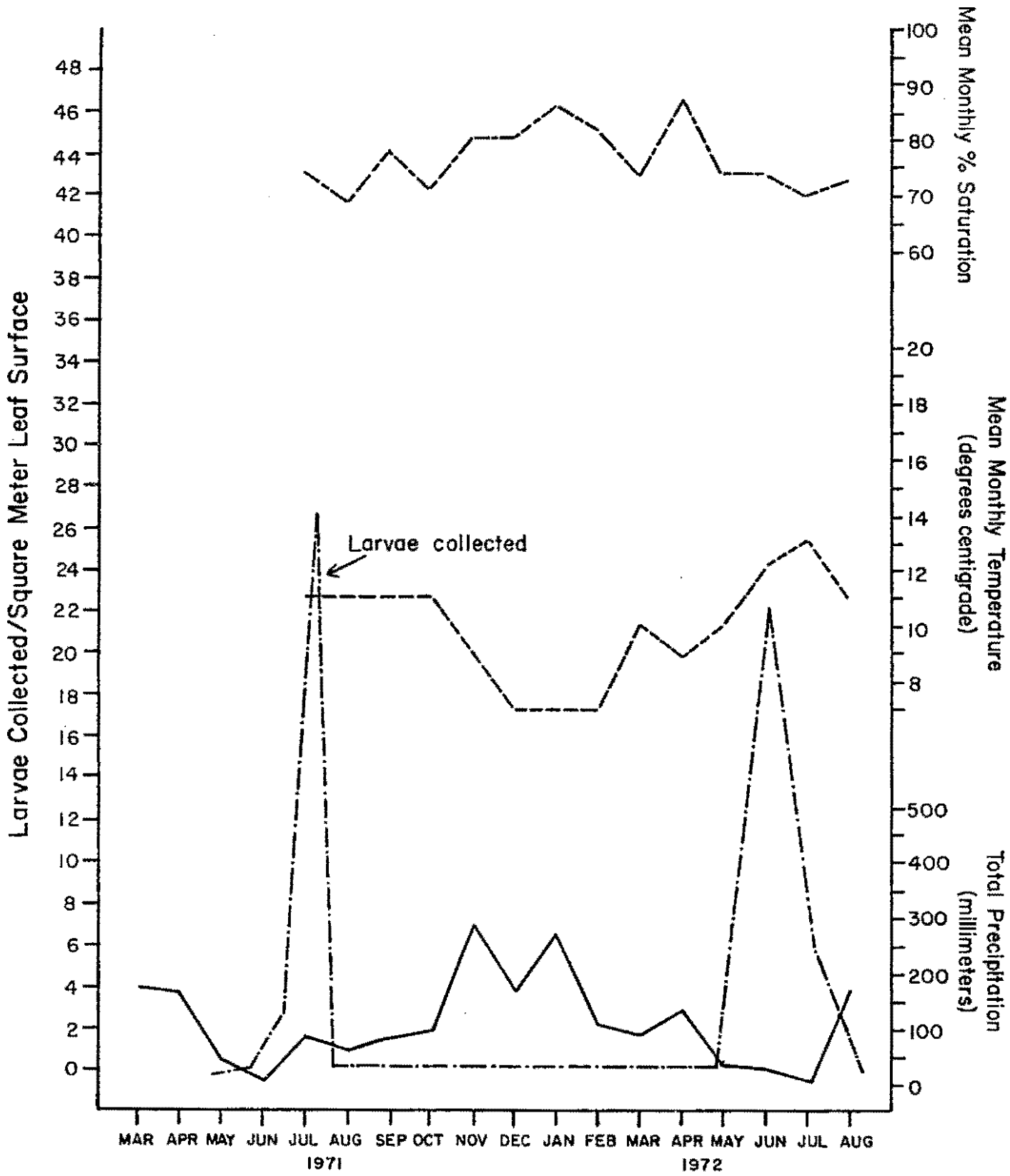

FIG. 2. Seasonal abundance of U. polygonalis larvae on mamane trees, total precipitation, mean monthly temperatures, and monthly humidity, means at site 1, 2010 m (6600 ft), Mauna Loa Strip Road, 1971-72. Precipitation, temperature and humidity data are taken from the meteorological records of the U. S. International Biological Program and the National Park Service.

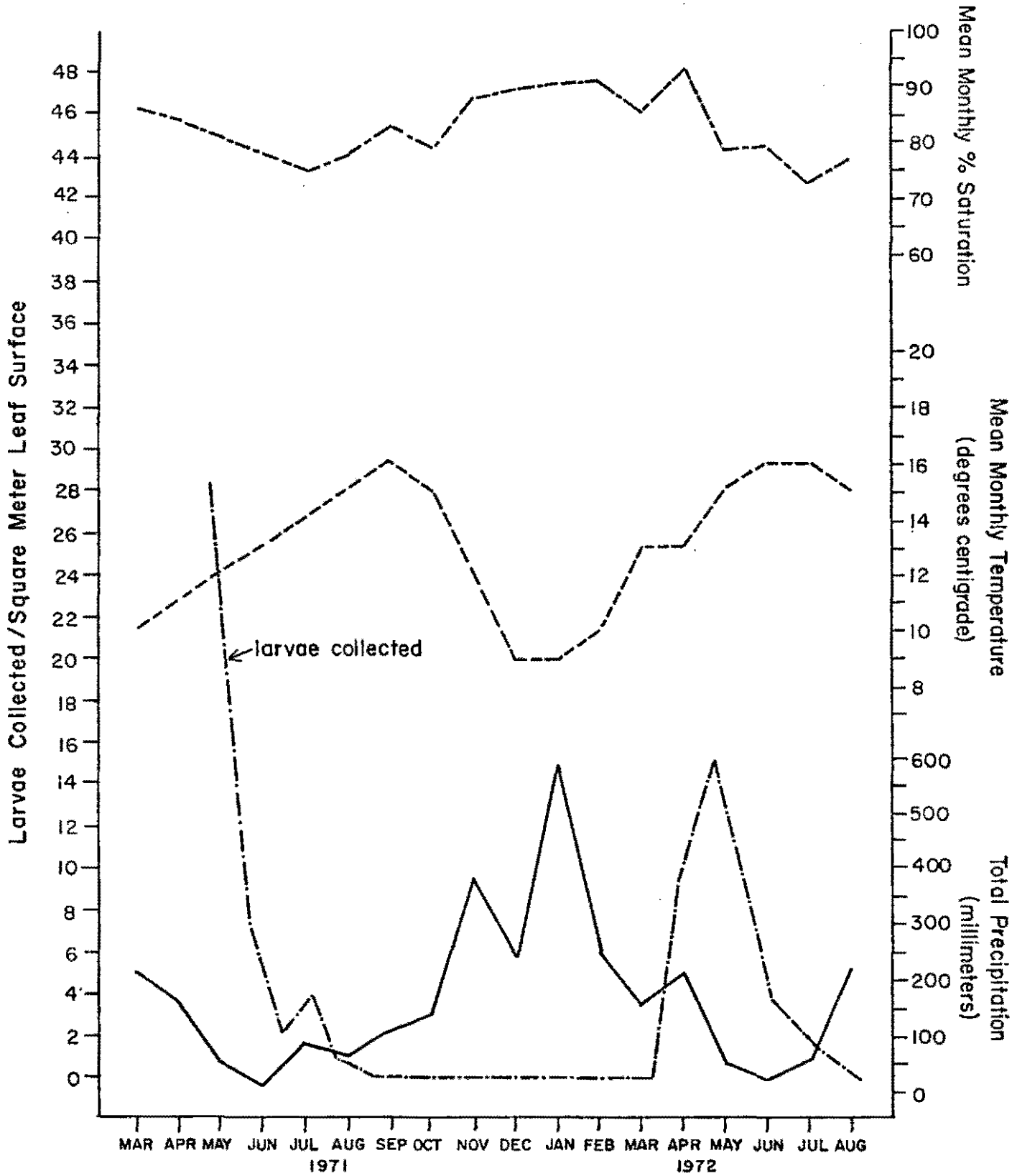

FIG. 3. Seasonal abundance of U. polygonalis larvae on the mamane trees, total precipitation, mean monthly temperatures, and monthly humidity, means at site 2, 1650 m (5400 ft), Mauna Loa Strip Road, 1971-72. Precipitation, temperature and humidity data are taken from the meteorological records of the U. S. International Biological Program and the National Park Service.

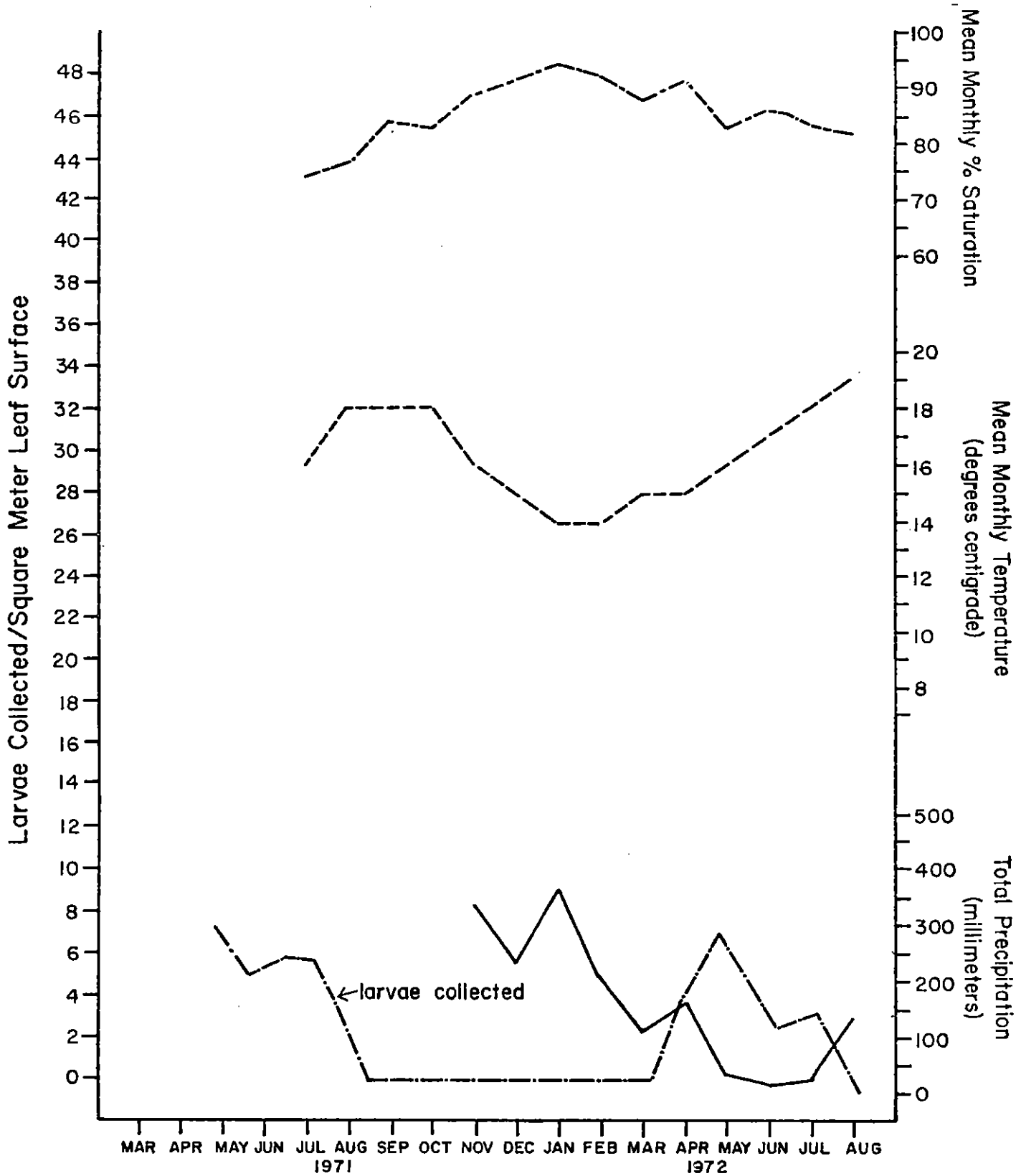

FIG. 4. Seasonal abundance of U. polygonalis larvae on mamane trees, total precipitation, mean monthly temperatures and monthly humidity, means at site 3, 1280 m (4200 ft), Mauna Loa Strip Road, 1971-72. Precipitation, temperature and humidity data are taken from the meteorological records of the U. S. International Biological Program and the National Park Service.

saturation (relative humidity) means were derived from hygrothermograph recordings. The mean monthly temperatures and percent saturation means are true means; the sum of the readings for every 2 hours during the month was divided by the number of readings. There were no rainfall, temperature, or humidity measurements available for site 4 which was located on Mauna Kea in a pasture.

Rainfall records were not available for site 3 until November, 1971. Temperature and humidity records at sites 1 and 3 were not taken until July, 1971. Records for these factors were taken at 2210 m (6600 ft) for site 1, 1650 (5400 ft) for site 2, and 1280 m (4200 ft) for site 3.

At site 1 in 1972 (Figure 2), the larval counts were the highest at the start of June when the first larvae appeared in samples for that year. The average humidity for this period was 74 percent. The humidity readings were the same in May, but higher (88 percent) in April. The July sample showed a decline in larval numbers and a drop in humidity to 70 percent. In August no larvae were taken.

At site 2 the humidities averaged 85, 83, and 80 percent respectively for March, April and May, 1971 and hovered around the mid 70's for the summer months. The highest larval count was recorded at the end of April after which the population declined. In 1972, the humidities for March through August were 85, 93, 78, 79, 73, and 77, respectively. The larvae increased substantially in March, continued to increase in April to a high for the year at the end of that month and then declined from May through July until none were collected in August.

Site 3 relative humidities for the months when the larvae were most active were 88, 91, 82, 86, and 84 percent for March through July, respectively. Larval populations increased in March and April reaching the highest numbers at the end of April. No larvae were collected in samples after mid-August.

The rainfall at all three sites showed the same general trends. Most of the rainfall occurs from October through April.

The low temperatures occurring at site 1 apparently did delay the appearance of U. polygonalis. Larvae were not collected until June in one year and in May in the following year. The threshold temperature for development appears to lie between 8° and 9°C. Once the threshold was crossed, however, there was a very rapid increase to a very high level.

At site 2 in 1971 the highest larval counts were recorded in April and May--months that had mean temperatures of 11°C and 12°C, respectively. The 1972 high again occurred at the end of April which had a mean of 13°C that year. Larvae were collected in samples from March until August.

At site 3, the average temperature did not drop below the minimum development temperature for U. polygonalis at any time of the year but again larvae were collected in samples only from March until August. It is apparent that temperature could be limiting if it were below the developmental threshold, but once it passes the threshold, other factors dictate the appearance or disappearance of larvae of U. polygonalis.

A careful analysis of the humidity and rainfall data also reveals no obvious correlations between the populations of U. polygonalis and humidity or rainfall. Humidities remained rather uniform, between 75 and 90 percent, throughout most of the year and apparently was not a limiting factor.

Although rainfall was generally low during May, June, and July when peak populations of U. polygonalis were present, the populations started building in March and April when the rainfall was still high and disappeared in August when the rainfall was at about the same level as in March.

Rainfall, however, could directly affect the vegetative flush of mamane and indirectly affect U. polygonalis populations in this manner. Therefore, attempts were made to correlate the vegetative flushing of mamane with the occurrence of U. polygonalis. For this, data obtained by Lamoureux (1973) on the vegetative flushing of mamane on the Mauna Loa Strip Road, the same area as the sampling sites, were used. Figures 5, 6, and 7 present this analysis.

At site 1, there seemed to be a correlation between vegetative flush and U. polygonalis, at least in 1971. In 1972, however, the mamane flushed and the index was declining when the U. polygonalis population started to increase. At site 2, the synchrony seemed to be in 1972, and the asynchrony in 1971. The relationship of vegetative flushing to U. polygonalis populations at site 3 was similar to that at site 2.

Significantly, however, mamane seems to have flush growth throughout most of the year and larvae were collected at site 3 in the absence of flush growth. The data seem to indicate, therefore, that the availability of flush growth was not a limiting factor in the population increase of U. polygonalis.

It is obvious that factors other than those analyzed--temperature, humidity, rainfall, and vegetative flush--play a major role in the appearance of U. polygonalis. Very significant is the fact that the populations declined rapidly at all elevations in August and reappeared in March if the temperature rose above the developmental threshold. This has happened at all sites in both 1971 and 1972. Since temperature, rainfall, and vegetative flush all differed at

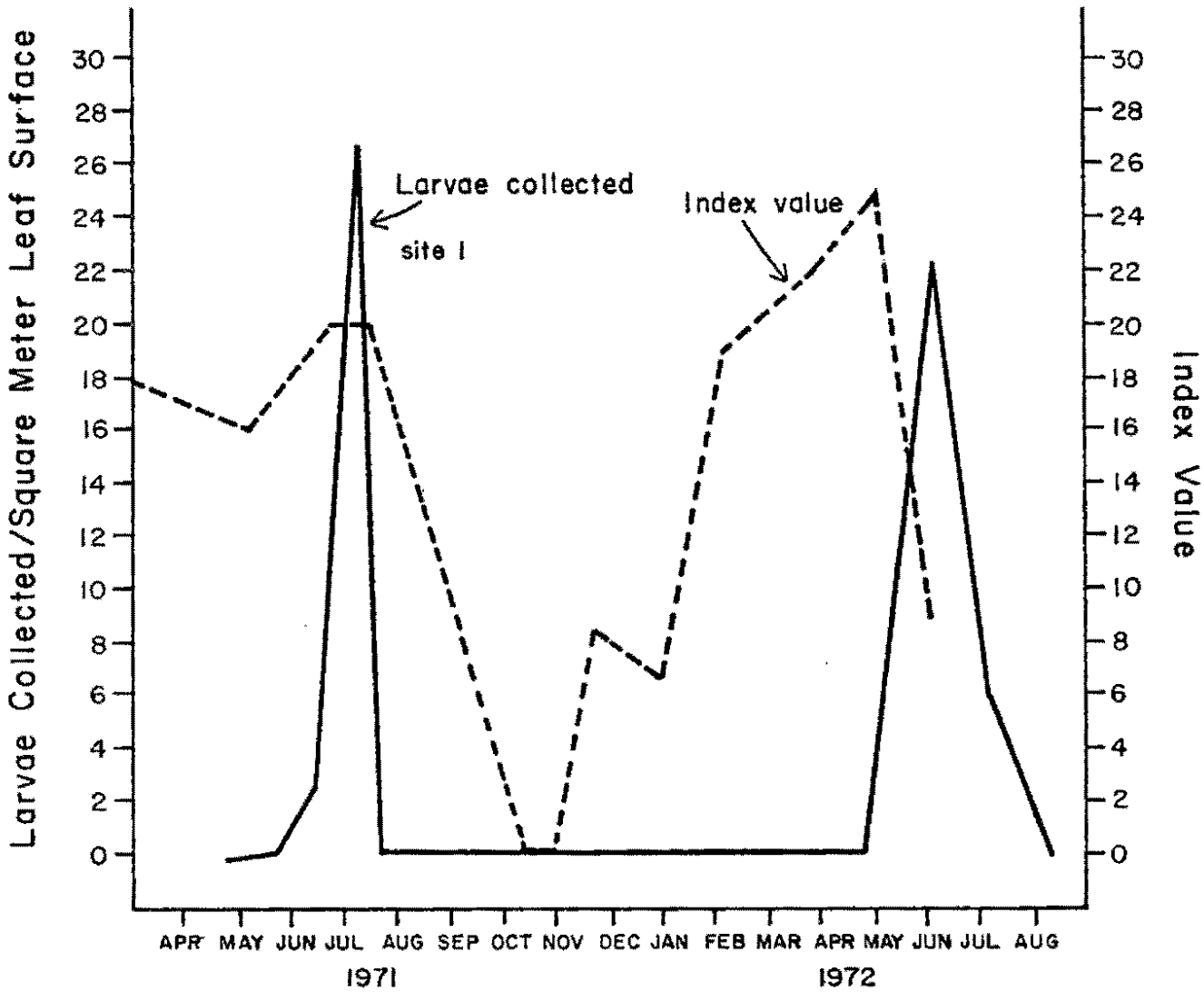

FIG. 5. The relationship between vegetative flushing of mamane and seasonal abundance of U. polygonalis at site 1.

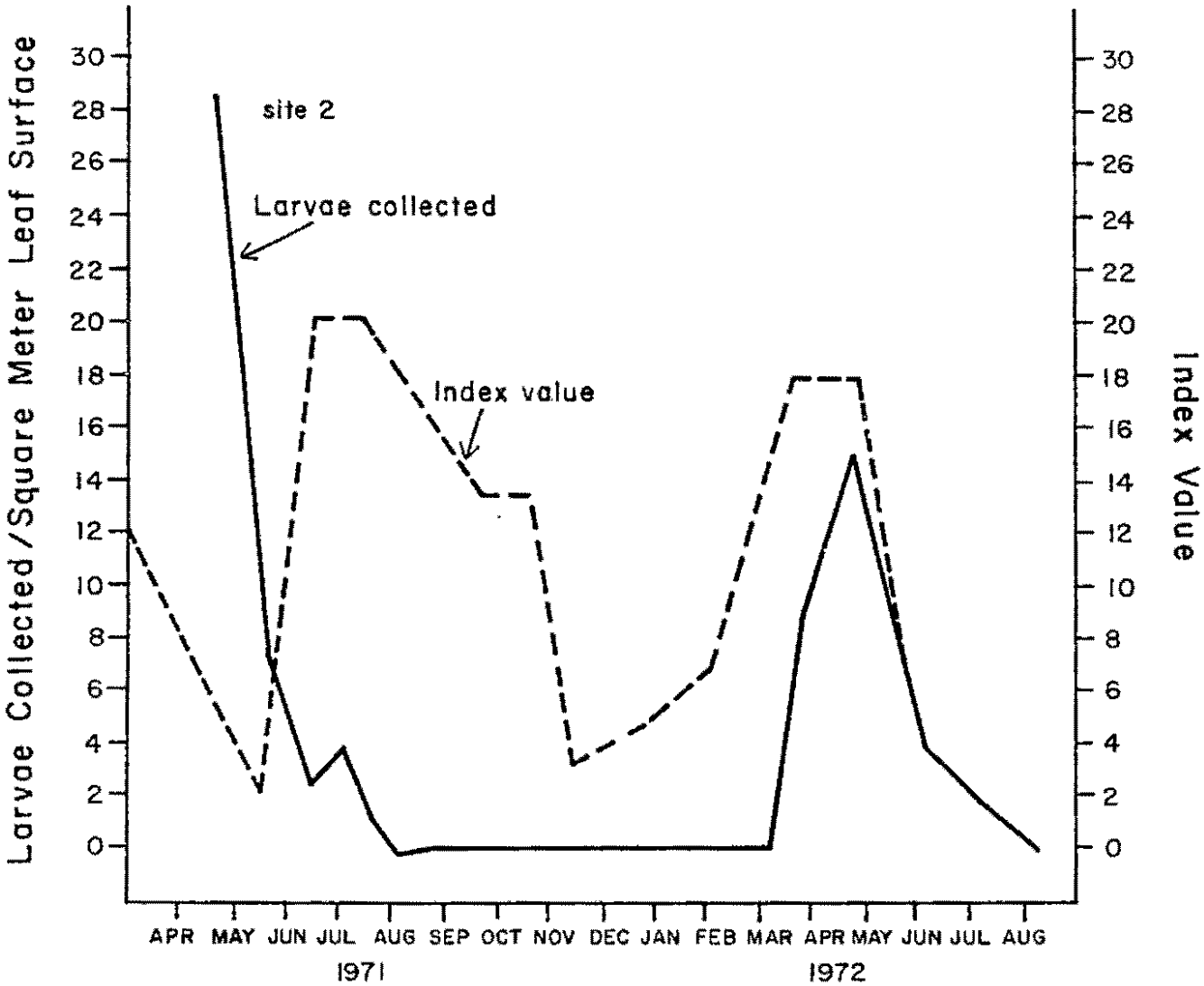

FIG. 6. The relationship between vegetative flushing of mamane and seasonal abundance of U. polygonalis at site 2.

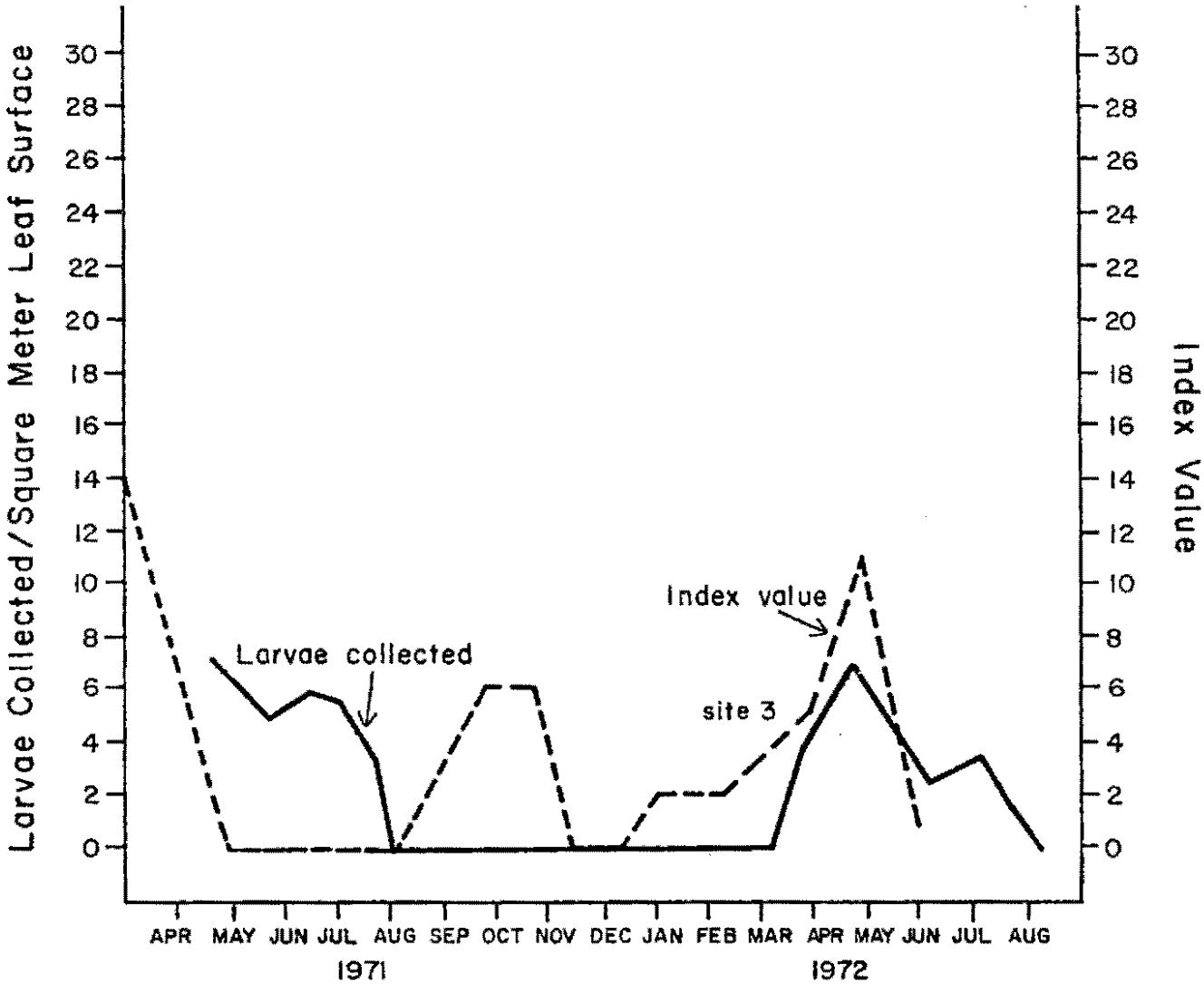

FIG. 7. The relationship between vegetative flushing of mamane and seasonal abundance of U. polygonalis at site 3.

the three sites in August, some factor or factors either intrinsic to the insect such as biological rhythm or factors extrinsic to the insect such as day length or a combination of these factors were responsible for the presence or absence of U. polygonalis.

Natural Control

Four parasites--a tachinid, two ichneumonids and a Trichogramma--were reared from U. polygonalis collected at the sampling sites. General predators, such as spiders, and an endemic pentatomid were also observed feeding on the larvae of U. polygonalis. A NPV was also found although it occurred only in those larvae collected at site 4 on the Saddle Road. Table 2 lists the natural control agents observed. None except the NPV played a significant role in the regulation of the populations of U. polygonalis.

Lespesia archippivora (Riley), a parasite of many lepidopterous larvae, was introduced from North America. It parasitizes larvae from at least nine different families of Lepidoptera (Bryan, Jackson and Patana, 1968). It is now widely distributed in the Hawaiian Islands (Kamran, 1968). The adults are small gray flies, 4-8 millimeters long. The female oviposits a small egg on the surface of the larva, the egg hatches in minutes and the 1st instar parasite bores through the body wall of the host. The maggot passes through 3 instars and at the end of the last, it cuts through the host's body wall and pupates on the substrate. The adult flies emerged from the puparia in about 8 days.

With U. polygonalis the fly parasitizes larvae that are third instar or older. Therefore, in calculating the percentage parasitism for this insect, the number of 1st- and 2nd-instar larvae were excluded from the calculations.

A parasitized host became increasingly sluggish as the maggot matured. When mature, it looked like a tumor pushing out against the host wall. The parasite cuts a slit in the host wall to exit. Because of blood coagulation and tanning, the exit point appears as a black lesion on the host's integument. The hosts were still alive when the parasites exited, but died shortly thereafter. Only one parasite matured per host larva.

L. archippivora were reared from larvae collected only from April until July although host larvae were active from March until August in most of the sites. Moreover, parasitism was at a relatively low level at all sites (Figures 8, 9, 10, 11). A maximum of 23 percent parasitism was recorded at site 2 in May, 1971. In

TABLE 2. Biological control agents of U. polygonalis in Hawaii.

Name	Stage of Host Attacked			
	Egg	Larva	Pupa	Adult
Parasites				
Diptera: Tachinidae				
Lespesia archippivora		+		
Hymenoptera: Ichneumonidae				
Horogenes blackburni		+		
Pristomerus hawaiiensis		+		
Hymenoptera: Trichogrammatidae				
Trichogramma sp.	+			
Disease				
Virus: Nuclear Polyhedrosis of *U. polygonalis*		+	+	
Predators				
Spiders: Argiopidae		+		
Salticidae		+		
Hemiptera: Pentatomidae				
Oechalia bryani		+		

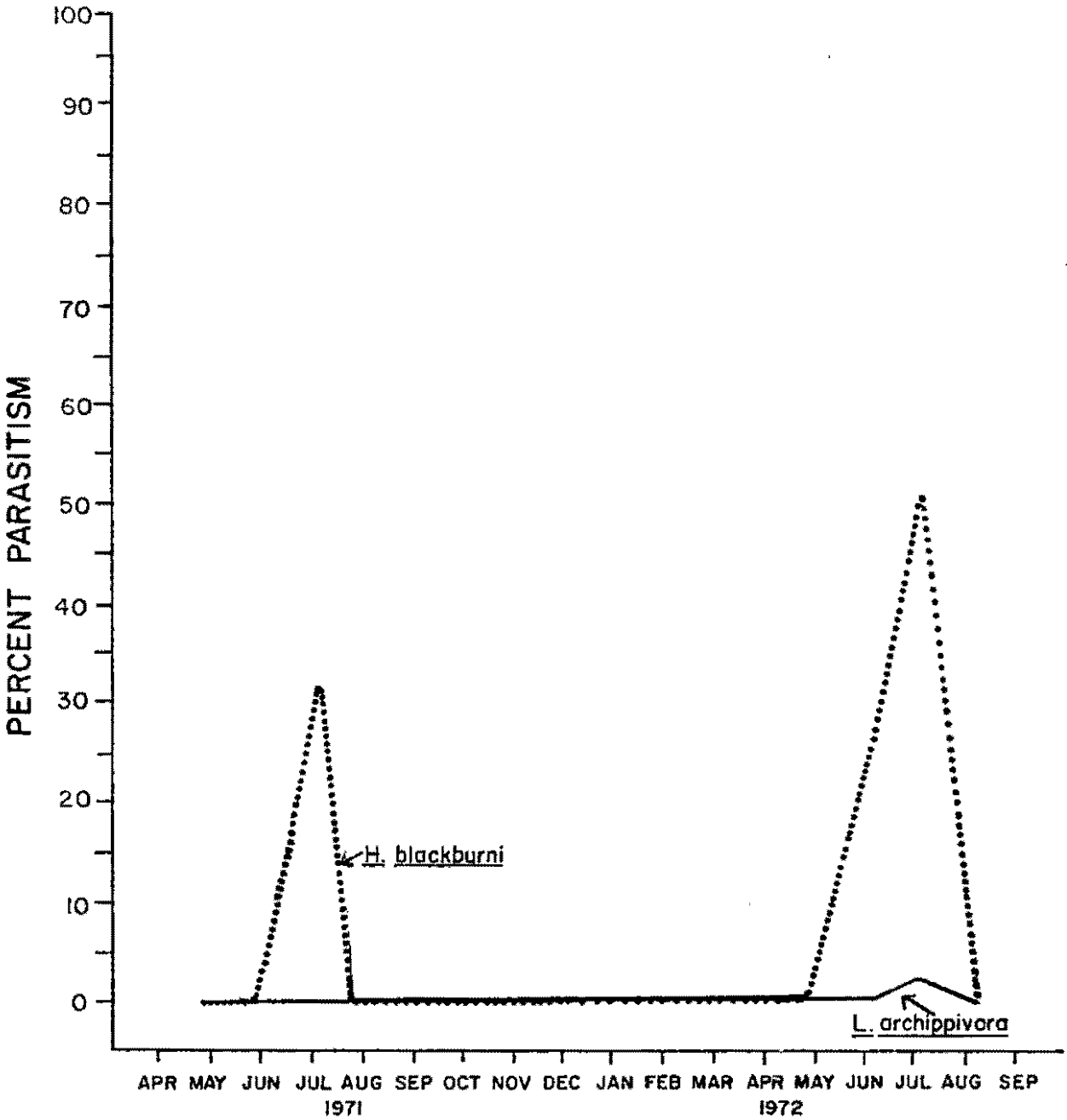

FIG. 8. Percent parasitism of U. polygonalis by 2 species of major parasites at site 1, 2210 m (6600 ft) elevation, Mauna Loa Strip Road, 1971-72.

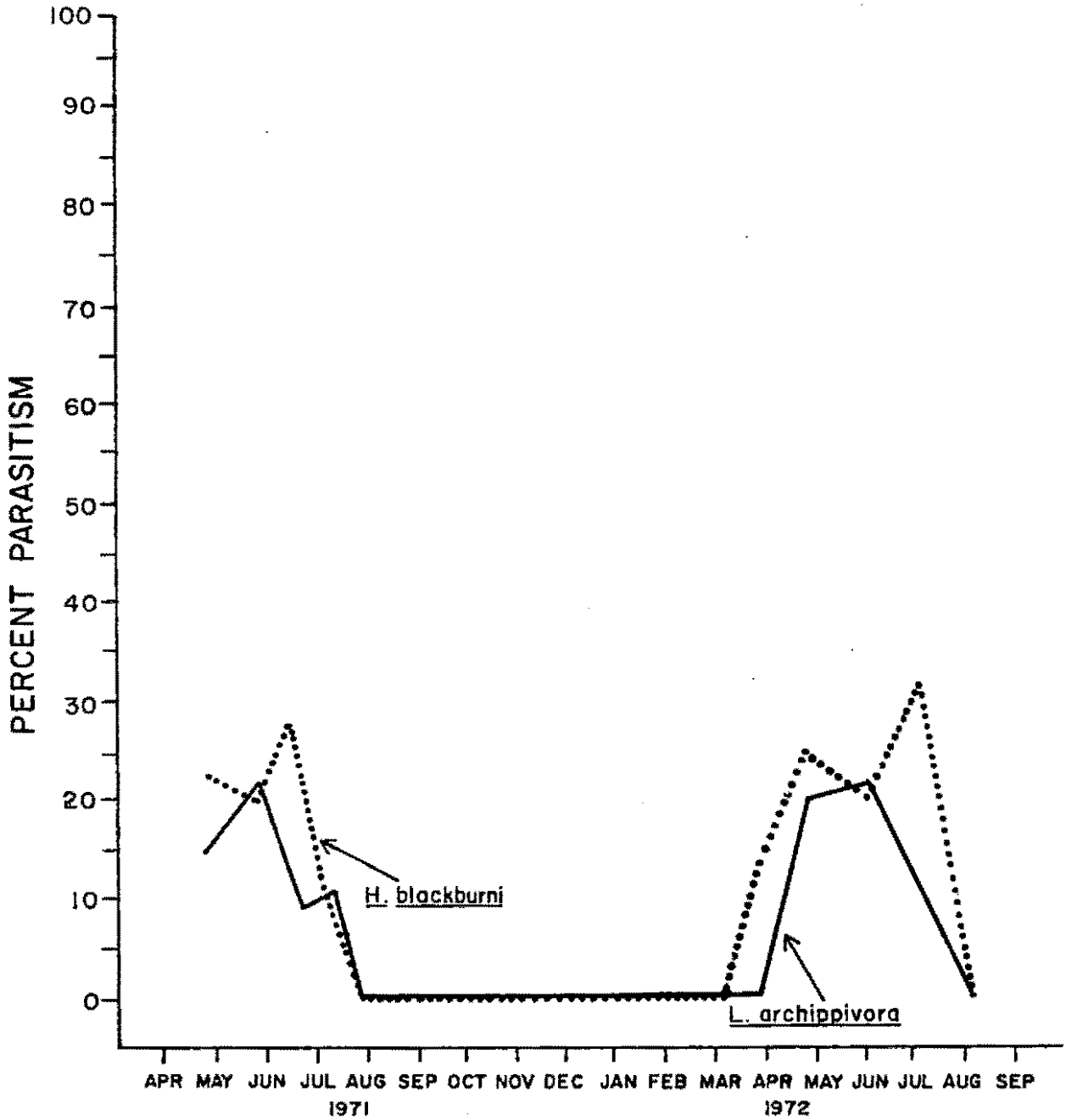

FIG. 9. Percent parasitism of U. polygonalis by 2 species of major parasites at site 2, 1650 m (5400 ft) elevation, Mauna Loa Strip Road, 1971-72.

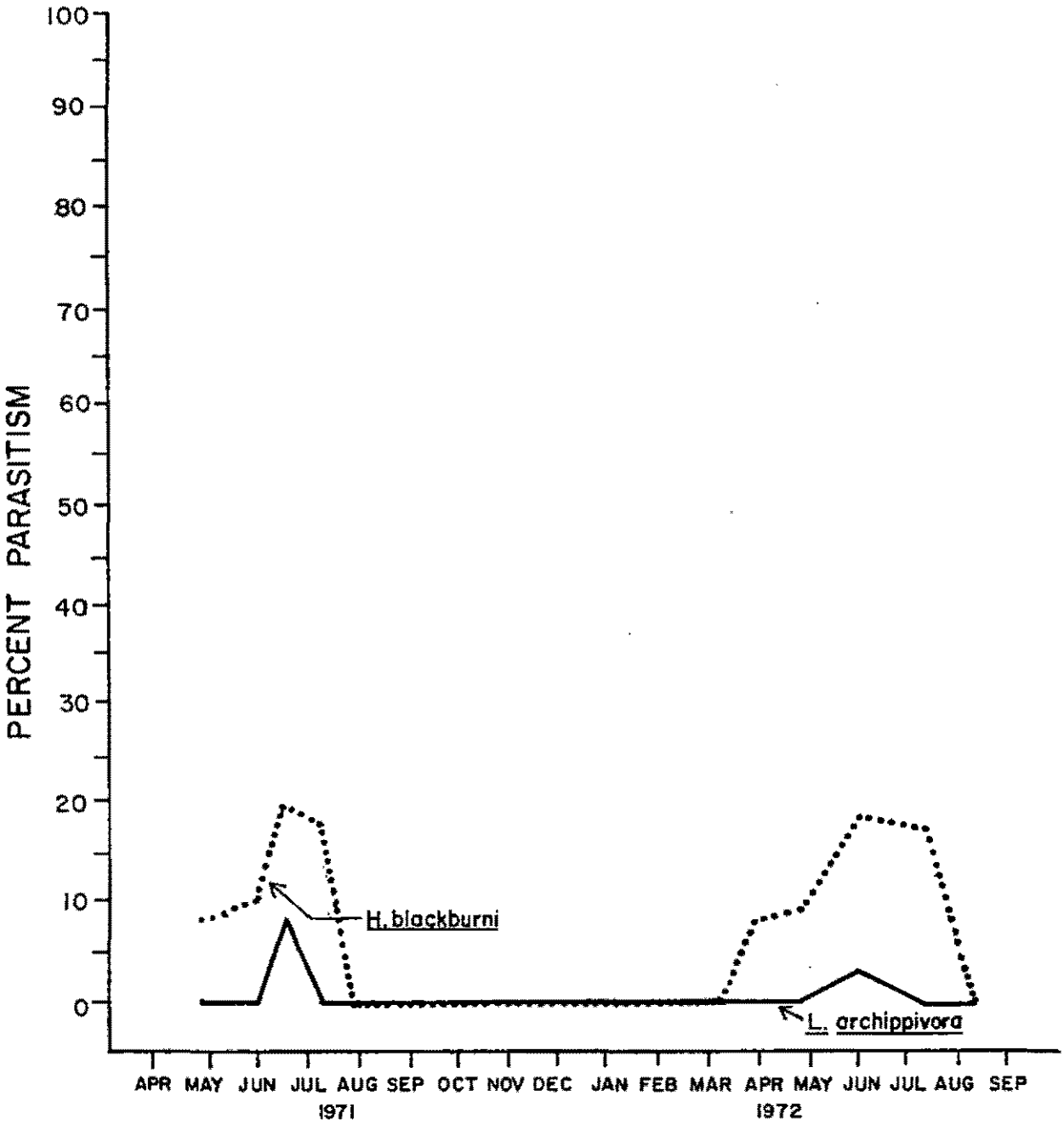

FIG. 10. Percent parasitism of U. polygonalis by 2 species of major parasites at site 3, 1280 m (4200 ft) elevation, Mauna Loa Strip Road, 1971-72.

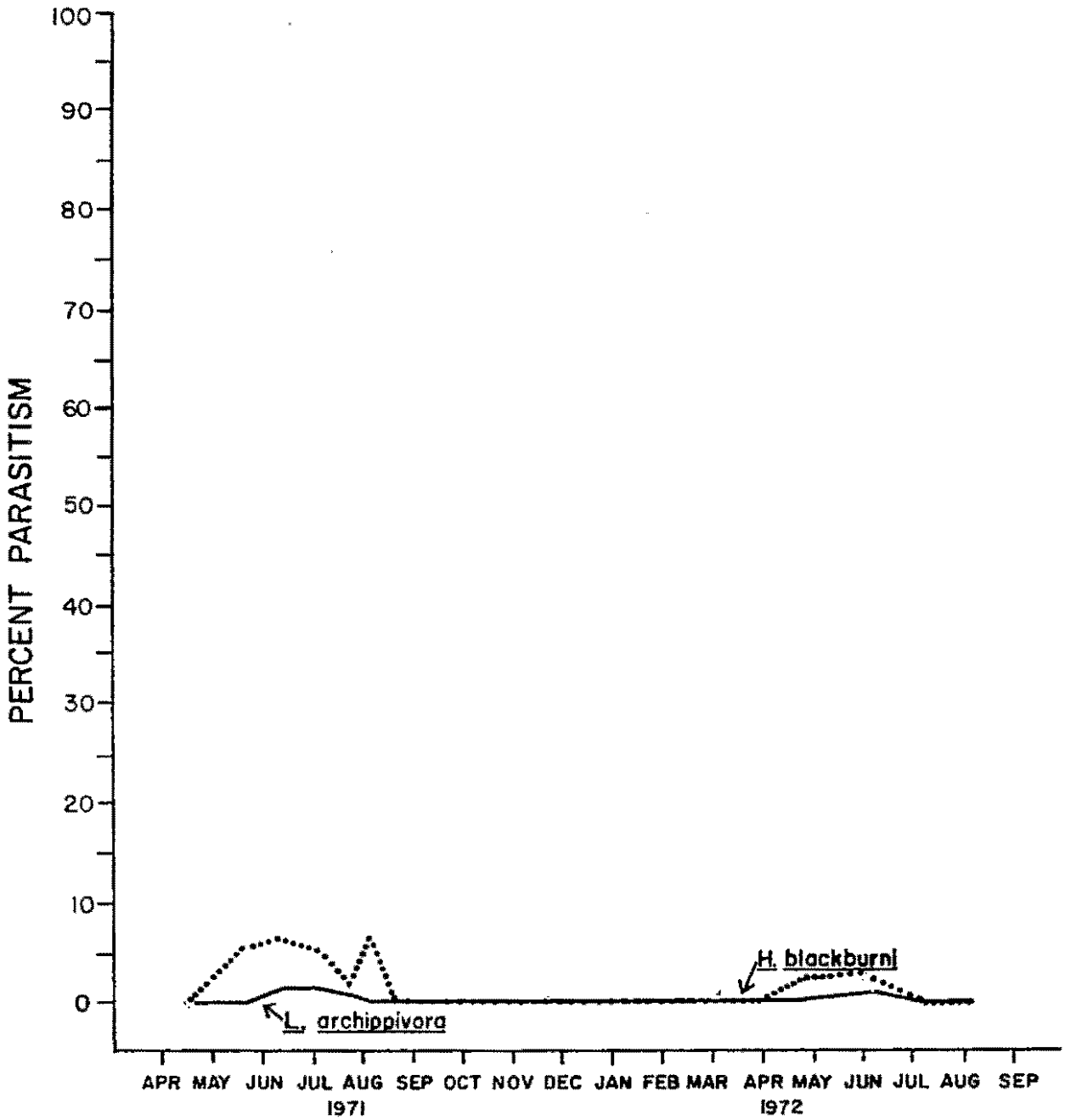

FIG. 11. Percent parasitism of U. polygonalis by 2 species of major parasites at site 4, 1680 m (5500 ft) elevation, Saddle Road, 1971-72.

general, however, parasitism by L. archippivora not only did not exceed 10 percent but generally remained below five percent.

Horogenes blackburni (Cameron), the other parasite that was reared in recordable numbers, is a small, black wasp 5 to 6 mm long. It was reared from larvae collected on Mauna Kea and Mauna Loa. The female oviposited in the 1st- and 2nd-instar larvae. The parasite larva took approximately 30 days to mature in U. polygonalis. The larval development of the host was prolonged, and even after 30 days the host was just in the 3rd or 4th instar. The mature parasite larva emerged from the host, spun a cocoon and pupated. The dead, shriveled host body was attached to the webbing of the cocoon. The pupa was brown with a white band around the middle and measured about 6 mm long. The adult emerged in about a week.

H. blackburni was the most prevalent and the most important parasite on U. polygonalis. It was present at all of the sites and in almost all of the samples (Figures 8, 9, 10, 11). Even in those few times when H. blackburni was not reared from the samples, the adults were observed actively searching the mamane. Parasitism by this ichneumonid reached a high of 50 percent of the 1st- to 4th-instar larvae collected at site 1 in July, 1972. Overall parasitism for site 1 was 36 percent; for site 2, 17 percent; for site 3, 11 percent and for site 4, 4 percent.

The data do not seem to indicate that there was sufficient pressure by this parasite to cause the collapse of host populations. The parasite populations apparently increased in response to increased availability of hosts but did not increase high enough or rapidly enough to regulate host populations. It did, however, probably moderate the height of the peaks in the host population.

The third parasite, Pristomerus hawaiiensis Perkins, parasitizes 1st- or 2nd-instar larvae. The mature parasite larva bored its way out of the 4th-instar caterpillar and spun a white cocoon with the dead host attached. In the cocoon it pupated, forming a light brown pupa about 8 mm long. Only three of these parasites were reared out of collected larvae. Their hosts were collected on Mauna Loa Strip Road.

Trichogramma sp., completely parasitized an egg mass containing 14 eggs and one containing 26 eggs collected at site 2 on June 15, 1971. The two egg masses appeared normal and were brought back to the lab for observation. The egg masses blackened after 3 to 4 days followed by emergence of small black parasitic wasps. These two were the only egg masses out of 46 collected which were attacked by this

parasite.

A major factor, where it was present, which regulated populations of U. polygonalis was the NPV. The virus was present in the population at site 4, either in an attenuated state or at an enzootic level. In a normal infection, contaminated leaves were eaten by a larva and the polyhedra were dissolved in the gut releasing the virus particles. The virions invaded the nucleus of some midgut cells. The virions multiplied and subsequently infected the nuclei of the fat bodies, tracheal matrix, silk glands, Malpighian tubules, and the epidermis, eventually filling the entire body causing the larva to become opaque white. As the disease progressed, the larva became sluggish and ceased to feed. The larva eventually became an extremely fragile sac containing virus particles and polyhedra. The body wall then ruptured releasing millions of polyhedra over the surrounding foliage. Transmission was effected when another larva ingested some of the polyhedra that had spilled on mamane leaves. The time from the ingestion of the polyhedra until death varied with the amount of polyhedra consumed, the age of the larva, environmental factors such as temperature, and crowding. Larvae usually were the victims but occasionally the disease carried over and killed the insect after it pupated. On rare occasions adults were found dead with polyhedra in their tissues.

The virus consistently infected and killed more than 80 percent of the larvae collected (Figure 12). During the winter months, September to March, when populations of U. polygonalis were very low (none were collected in the samples; the few larvae which were found were either in the shrubbery, under rocks at the base of the tree, or in the tree) all came down with the virus disease. However, since the larvae were all brought back to the laboratory and reared, there was a possibility that stress factors such as change in temperature, container size, food, etc., may have contributed to the activation of an attenuated infection. It was significant that the virus seemed to be present in an attenuated state in the entire population that over-wintered. The virus was always present in a high enzootic state at site 4.

The surprising thing, however, was the fact that the virus was found only at site 4 on the Saddle Road. The virus was originally found by Clifford J. Davis, State Entomologist (pers. comm.), on the island of Hawaii in the Kamuela area. Site 4 was in a pasture with scattered groves of mamane and was located near Kilohana on the Kamuela end of the Saddle Road.

The reason why the virus did not appear in all of the sample areas was

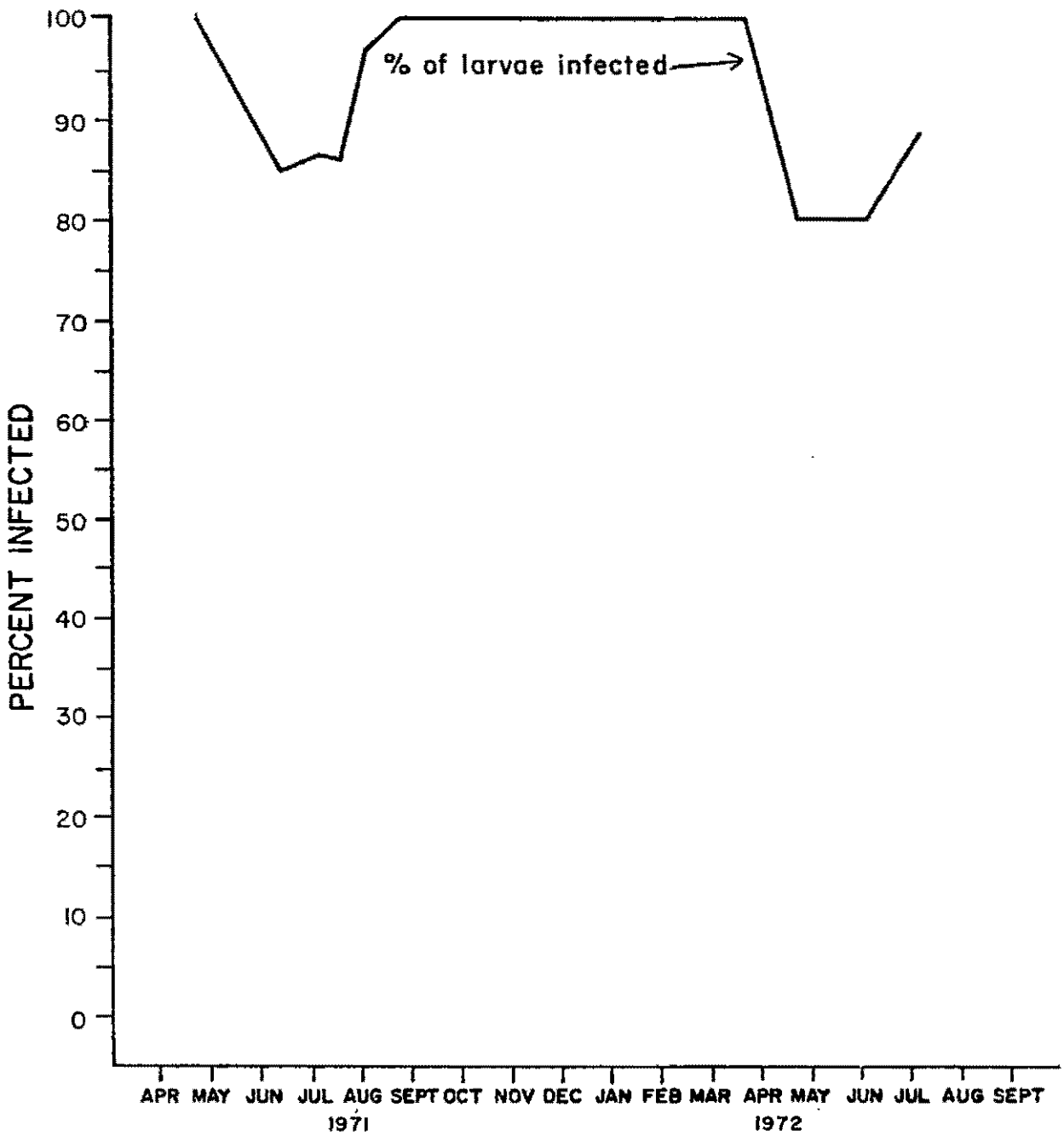

FIG. 12. The percentages of larvae that were infected with and died from a nuclear polyhedrosis virus at site 4, 1680 m (5500 ft) elevation on Saddle Road, 1971-72.

difficult to explain. Laboratory tests indicated that larvae of U. polygonalis from all areas were highly susceptible to the virus. Moreover, mamane and presumably populations of U. polygonalis occur in a more or less continuous belt around the mountain. Over the saddle, however, there was an apparent break in the population.

The U. polygonalis populations declined sharply between Kilohana (1710 m or 5600 ft) near site 4 and Pohakuloa (1950 m or 6400 ft). None were sighted a mile past Kilohana. Feeding damage was observed past this point, but further up the Saddle Road the damage also abruptly ended. The characteristic webbing was never seen at Pohakuloa indicating a break from the Mauna Loa population.

In the direction of Hualalai the mamane trees of Mauna Kea separated into fingerlike projections that end in a few scattered trees. The break between the mamane of Mauna Kea and the mamane of Hualalai may restrict the movement of U. polygonalis across to Hualalai, although the flight range of the adult may enable it to fly between mamane clumps. The flight range of U. polygonalis is not known.

In addition, there may have been differences in physical factors, especially in the amount of sunlight and ultraviolet irradiation reaching the trees and the ground. Although no data are available, gross observations made during the many visits to the sites indicate that site 4 generally had cloud cover and fog while the others did not. The sunny areas separating Mauna Kea from Mauna Loa and Hualalai may have restricted movement of the virus from site 4.

The nuclear polyhedrosis viruses like many other insect pathogens are readily inactivated by sunlight, especially by the ultraviolet component. This may in part explain the absence of the virus along the strip road and in the upper reaches of the Saddle Road. Therefore, in years when U. polygonalis populations do not reach high levels, the virus was confined to areas such as site 4. The virus was not recovered in any other part of the island although it was actively sought.

However, in years when U. polygonalis populations reach outbreak levels, years in which they can completely strip the tree of leaves, these enzootic foci may serve as sources of virus inoculum to initiate major virus epizootics. That there were major virus epizootics covering large areas under these conditions was observed by C. J. Davis (pers. comm.).

The virus disease, therefore, plays a major role in population regulation, when the population reaches epizootic levels. This is similar to the role played

by many viruses in the regulation of insect populations.

Predators

Different species of orb weaving spiders were seen with larvae trapped in their webs. Predaceous native pentatomids, Oechalia bryani Usinger, were observed feeding on larvae at site 4 three times. Neuropterans were often present on the trees but were never seen preying on larvae.

It is obvious that none of the natural control agents observed, with the possible exception of the virus at site 4, played a significant role in the regulation of U. polygonalis populations in the study areas. The parasites and predators did not seem to have a significant effect on the fluctuations of the host populations.

Since both the major physical factors and the natural control agents apparently were not limiting factors for population increase during most of the year, other factors such as biological rhythm, day length, presence or absence of adult food, etc., were involved. The factor or factors, however, appear to operate at all elevations under various physical and biotic conditions at the same time.

SUMMARY AND CONCLUSIONS

The mamane moth, Uresiphita polygonalis (Denis and Schiff.) is a serious pest of the mamane tree, Sophora chrysophylla (Salisb.), on the island of Hawaii. U. polygonalis larvae feed on the mamane leaflets. Continued attack has often resulted in complete defoliation of young trees and serious defoliation of older ones.

The life cycle and description of stages were determined by observing generations of U. polygonalis reared in the laboratory. Attempts to raise U. polygonalis larvae on two artificial diets failed. Results of laboratory tests indicated that A. koa was not a host of the larvae.

Data on U. polygonalis seem rather sparse and scattered. Very little is known about the insect's seasonal abundance and the factors which influence it. The seasonal abundance of U. polygonalis was estimated from monthly counts of eggs and larvae captured in samples from four sampling sites. For each site abundance was plotted against monthly precipitation, monthly humidity means, mean monthly

temperatures and index values for vegetative flushing of mamane. A careful analysis of these data reveals no obvious correlations between these factors and the population fluctuations of U. polygonalis.

Four parasites--a tachinid, two ichneumonids and a Trichogramma--were reared from U. polygonalis collected at the sampling sites. The tachinid population was at relatively low levels at all sites. One of the ichneumonids, Horogenes blackburni (Cameron), was the most prevalent and the most important parasite on U. polygonalis. The data do not seem to indicate that there was sufficient pressure by this parasite to cause the collapse of host populations. The other ichneumonid and the Trichogramma populations were at very low levels.

A major factor, where it was present in the regulation of populations of U. polygonalis, was the nuclear polyhedrosis virus. The virus consistently infected and killed more than 80 percent of the larvae collected at site 4. The reason why the virus did not appear in all of the sample areas was difficult to explain. Laboratory tests indicated that larvae of U. polygonalis from all areas were highly susceptible to the virus. Moreover, mamane and presumably populations of U. polygonalis occur in a more or less continuous belt around the mountains.

There may be differences in physical factors, especially in the amount of sunlight and ultraviolet irradiation reaching the trees and the ground. The nuclear polyhedrosis viruses, like many other insect pathogens, are inactivated by sunlight. Therefore, in years when U. polygonalis populations do not reach high levels, the virus is confined to cloud covered areas such as site 4. However, in years when U. polygonalis populations reach outbreak levels, these enzootic foci may serve as sources of virus inoculum to initiate major virus epizootics. There have been major virus epizootics covering large areas under these conditions. The virus disease, therefore, plays a major role in population regulation, when the population reaches epizootic levels. All the factors analyzed did not seem to play a significant role in the population regulation.

ACKNOWLEDGEMENTS

I would like to thank Drs. Minoru Tamashiro, John W. Beardsley and Ryoji Namba for reading and commenting on the manuscript.

REFERENCES

Berger, Andrew J. 1972. Hawaiian Birdlife. Univ. of Haw. Press. Honolulu. pp: 122, 124-133, 145-147, 182-187, 222-225, 229.

Bridges, Kent W. and G. Virginia Carey. 1973. The Climate of the IBP Sites on Mauna Loa, Hawaii. US/IBP Island Ecosystems IRP. Tech. Report No. 22. Supplement 1: 41-54, 63-84, 89-102, 122-133.

Bryan, D. E., C. G. Jackson and Raymond Patana. 1968. Laboratory Studies of Lespesia archippivora in Four Lepidopterous Hosts. J. Econ. Ent. 61(3): 819-823.

Chock, Alvin K. 1956. A Taxonomic Revision of the Hawaiian Species of the Genus Sophora Linnaeus (Family Leguminosae). Pac. Science 10: 136-158.

Degener, Otto. 1945. Plants of Hawaii National Park Illustrative of Plants and Customs of the South Seas. pp: 179-182.

Degener, O. and I. 1971. Sophora in Hawaii. Phytologia 21(6):411-415.

Gressitt, J. L. and C. J. Davis. 1972. Seasonal Occurrence and Host-Lists of Hawaiian Cerambycidae. US/IBP Island Ecosystems IRP. Tech. Report No. 5: 17, 24, 31-33.

Hamm, John J. 1966. A Modified Azan Staining Technique for Inclusion Body Viruses. J. Insect Path. 8: 125-126.

Hanneman, J. M. 1964. Kleinschmetterlinge oder Microlepidoptera. II: Die Wickler (s.l.) (Cochylidae und Carposinidae): Die Zunslerartigen (Pyraloidea). Die Tierwelt Deutschlands 50: 332.

Kamran, M. A. 1968. Seasonal fluctuations in the Abundance of the Monkeypod Moth Polydesma umbricola in Hawaii. J. Econ. Ent. 61(4): 1011.

Lamoureux, Charles H. 1973. Phenology and Growth of Hawaiian Plants, a Preliminary Report. US/IBP Island Ecosystems IRP. Tech. Report No. 24: 17, 20-21.

Neal, Marie C. 1965. In Gardens of Hawaii. Bishop Museum Press. Spec. Pub. 50: 442-443.

Perkins, R. C. L. 1913. Introduction. Fauna Hawaiiensis. Cambridge Univ. Press. David Sharp Ed. clx.

Smith, Kenneth M. 1967. Insect Virology. Academic Press Inc. New York. pp: 9-21, 111-114, 128, 140-142, 150-152, 176-178, 188-190, 232-236.

Tompkins, G. L., J. R. Adams and A. M. Heimpel. 1969. Cross Infection Studies with Heliothis zea Using Nuclear-Polyhedrosis Viruses from Trichoplusia ni. J. Invert. Path. 14: 343-357.

van Riper, Charles, III. 1974. Linnet Breeding Biology on Hawaii. US/IBP Island Ecosystems IRP. Tech. Report No. 46: 1-6.

Wesson, L. G. 1932. A Modification of the Osborne-Mendel Salt Mixture Containing Only Inorganic Constituents. Science 75: 339.

Zimmerman, Elwood. 1948. Insects of Hawaii: Vol. III. Heteroptera. Univ. of Hawaii Press. Honolulu. 3: 38.

Zimmerman, Elwood. 1958. Insects of Hawaii: Vol. VIII. Lepidoptera: Pyraloidea. Univ. of Hawaii Press. Honolulu. 8: 115-118.

TECHNICAL REPORTS OF THE US/IBP ISLAND ECOSYSTEMS IRP

(Integrated Research Program)

*No. 1 Hawaii Terrestrial Biology Subprogram. First Progress Report and Second-Year Budget. D. Mueller-Dombois, ed. December 1970. 144 p.

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